Title

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Reply to Delmont and Eren: Strain variants and population structure during the *Deepwater Horizon* oil spill

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This article has a reply. Please see:

- Simulations predict microbial responses in the environment? This environment disagrees retrospectively
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A laboratory simulation revealed the succession patterns of oil degradation and microbial community changes during the *Deepwater Horizon* oil spill, one of the largest environmental catastrophes in human history (**1**). Hu et al. successfully recovered genomes of several oil-degrading bacteria, including one of "*Candidatus Bermanella macondoprimitus*," with high identity to the dominant *Oceanospirillales* 16S rRNA gene sequences recovered from the deep-ocean hydrocarbon plumes (**1**, **2**). Delmont and Eren (**3**) reanalyzed metagenomic data generated from these plumes (**4**) to argue that this *Bermanella* was not present.

We find that Delmont and Eren (**3**) draw their conclusions from methods that are flawed. Importantly, the authors (**3**) use samples that underwent an emulsion PCR (**4**) [according to Mason et al. (**4**) overloaded by ∼20 molecules per droplet (**5**)], which likely resulted in a heavy distortion of the sequenced community and observed abundance patterns (**6**). Delmont and Eren (**3**) failed to use any metagenome assembler that attempts to account for biases of amplified metagenomes and compounded the issue by applying a binning method that uses abundance information (**6**). The quality of their recovered genomes is poor: a genome of 1.6 Mbps without any single copy genes (**6**) and a highly fragmented and incomplete genome of the designated "dominant" organism called "*Oceanospirillales desum*" (***Fig. 1 A and B***). Notably, this dominant organism recruited only 15% of reads from the amplified metagenomic library of the proximal plume sample [stated as 77.8% of 19.7% of mapped reads (**6**)]. In contrast, the genome of the dominant organism of the simulation experiment, *B. macondoprimitus*, showed higher completeness (>99%) (**7**) and

substantially lower fragmentation, despite its great abundance in the dataset (***Fig. 1 A andB***) (**1**).

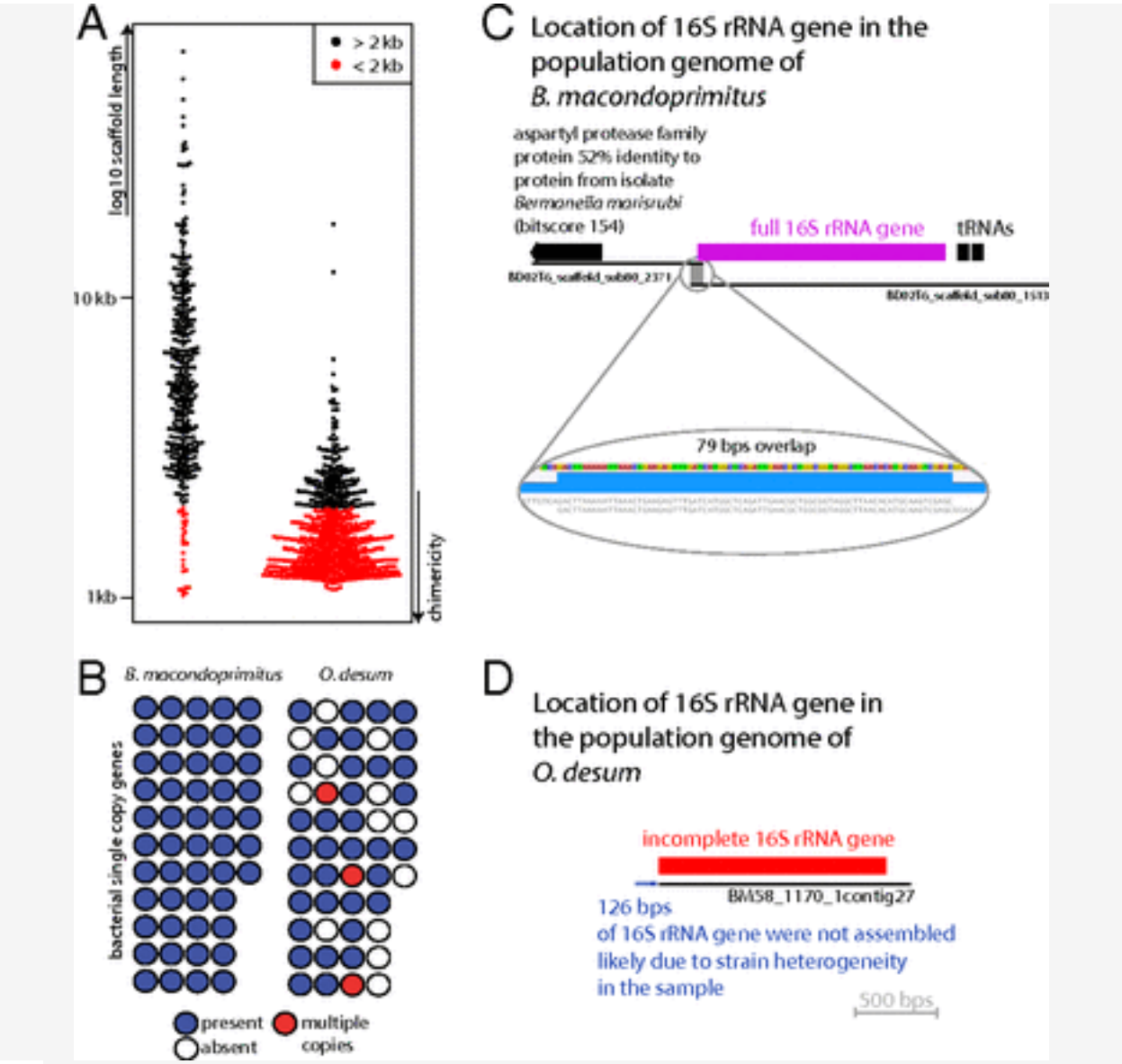

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Fig. 1.

(*A*) Scaffold-length distribution of population genomes *Candidatus B. macondoprimitus* (**1**) and *O. desum* (**6**). The high fragmentation rate of the latter has a greater risk for chimeric sequences (**10**): >70% of the scaffolds <2 kb. (*B*) Genome completeness of *Candidatus B. macondoprimitus* and *O. desum*.

Each circle represents one single-copy gene (**7**). The genome designated "*O. desum*" is incomplete and contains multiples of single-copy genes, likely a result of mixed assembly of different strains. (*C*) Scaffold location of the 16S rRNA gene of *Candidatus B. macondoprimitus*. (*D*) Contig location of the incomplete 16S rRNA gene of *O. desum*, which cannot be connected to the rest of the binned genome.

While the 16S rRNA gene of *B. macondoprimitus* can be linked to its genome via sequence overlaps (***Fig. 1C***), there is no evidence that the 16S rRNA gene attributed to *O. desum* is connected to its recovered genome (***Fig. 1D***). Detailed analysis of 16S rRNA gene sequences from the Gulf of Mexico (**2**, **8**, **9**) revealed a massive population heterogeneity of *Oceanospirillales* represented by 146 different genotypes in a single cluster (***Fig. 2A***), which group with *O. desum* and *B. macondoprimitus* (***Fig. 2A***). A large fraction of reads (38%) from the amplified metagenome (**4**) matched to *B. macondoprimitus*' predicted proteome (blastx, bitscore >50). Notably, both *O. desum* and *B. macondoprimitus* represent population genomes, and we discovered high 16S rRNA similarity (>99.99%) between strains in the simulation experiment and strains recovered from the oil plume (***Fig. 2B***). Amplified metagenomes used by Delmont and Eren (**3**) barely matched the *Oceanospirillales* single-cell genomes (<1%) (**6**), although recovered from the same environment (**4**). Thus, the datasets (**2**, **6**) used by Delmont and Eren (**3**) were generated from amplification of multiple genotypes of the same species, resulting in very fragmented genomes, and are ultimately not representative of the true population structure during the oil spill. In contrast, the high-quality *B. macondoprimitus* population genome detected in our laboratory simulation (**1**) represents a strain variant of the dominant *Oceanospirillales* that bloomed in deep-water oil plumes, and provides important insights into the capabilities of this uncultivated species.

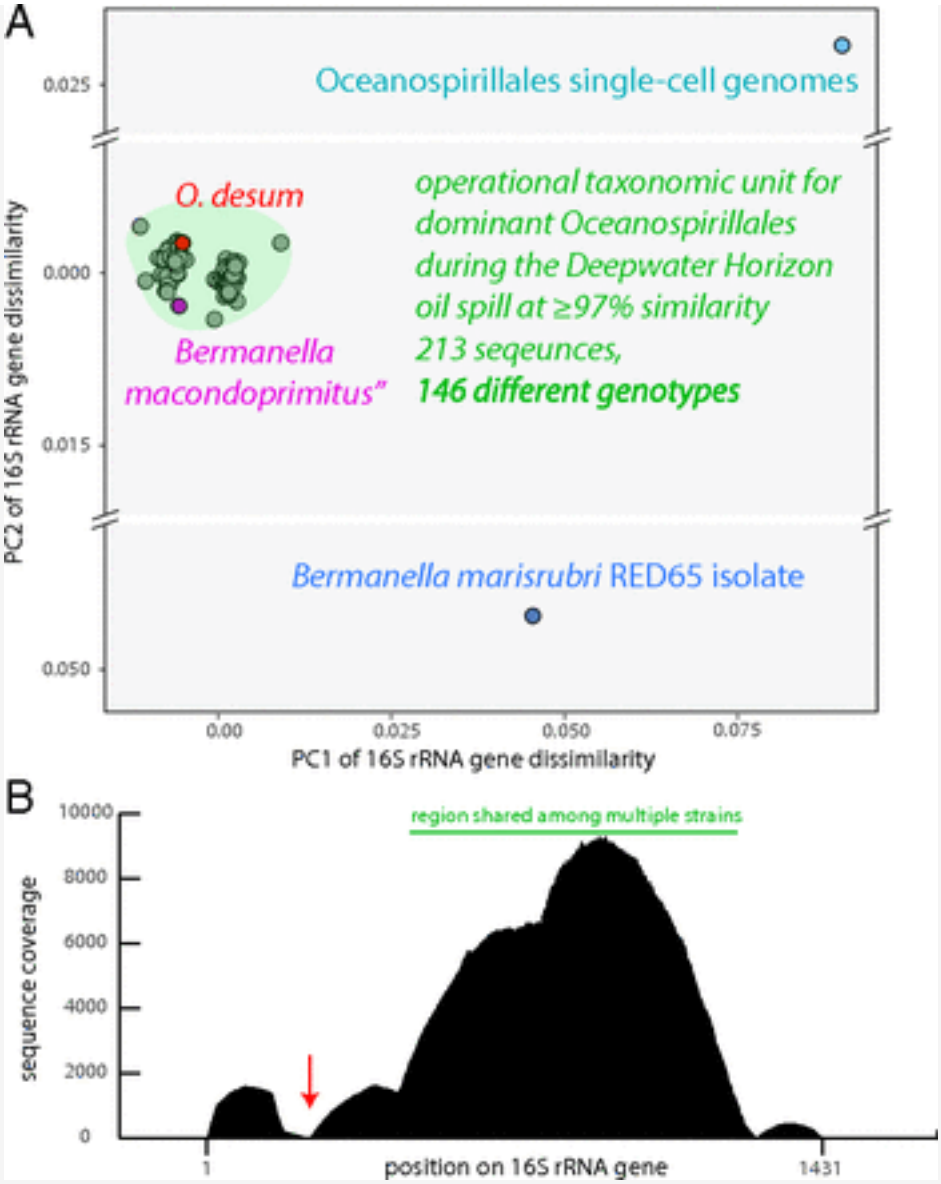

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Fig. 2.

(*A*) 16S rRNA gene diversity of the dominant *Oceanospirillales* species, *Candidatus B. macondoprimitus*, in the Gulf of Mexico during the *Deepwater Horizon* oil spill were retrieved from multiple studies (**2**, **8**, **9**) and included more than 150 novel 16S rRNA gene sequences from previous samples (**2**) (National Center for Biotechnology Information accession nos. MF571585–MF571832). (*B*) Agreement of reads from the

simulation experiment with a group of 16S rRNA gene sequences (one genotype) from the *Deepwater Horizon* oil plume (**2**). The paired-end reads show a near-complete coverage of the 1,431-bps region (red arrow points to a single base that was not covered).

Footnotes

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- Author contributions: A.J.P., P.H., E.A.D., and G.L.A. designed research; A.J.P. and C.L.S. performed research; A.J.P., P.H., E.A.D., and C.M.K.S. analyzed data; and A.J.P., C.L.S., E.A.D., J.F.B., and G.L.A. wrote the paper.

- The authors declare no conflict of interest.

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